THE DISTRIBUTION OF EARTHWORMS
(MEGASCOLECIDAE) IN RELATION TO SOILS,
VEGETATION AND ALTITUDE ON THE SLOPES OF MT
KOSCIUSKO, AUSTRALIA

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INTRODUCTION

The investigations described here were carried out on the eastern slopes of Mt Kosciusko, in the Snowy Mountains and are part of an extensive investigation of the soils and soil fauna of montane, sub-alpine and alpine habitats. This area, partly because of its intrinsic natural interest and relative ease of access and partly because of its location within the Kosciusko National Park, has long been of interest to naturalists and during the last 20 years, in particular, there has been considerable scientific interest in the region. Costin (1954) has presented detailed information on the climate, geology, soils and vegetation and more recent publications in the general field of soil science deal with land use and conservation (Costin 1959), catchment hydrology (Costin, Wimbush & Cromer 1964) and decomposition processes (Wood 1970, 1971).

Costin, Hallsworth & Woof (1952) studied the variation in soils and soil properties of an altitudinal sequence of soils developed on gneissic granite on the eastern slopes of Mt Kosciusko. They found that several soil properties achieved maximum development in the alpine humus soils of the upper sub-alpine and lower alpine zones between elevations of 1650 m and 1950 m (see also Table 2). This situation contrasts with many other soil-elevation relationships where soil properties vary in the same direction as altitude. However, it is the alpine humus soils, which are the climax soil in sub-alpine and alpine zones, that are of particular interest to the soil biologist. In common with most alpine and sub-alpine soils in other parts of the world, these alpine humus soils are acidic (pH 4–5), base-unsaturated (10 mEq/100 g O.D. soil), wet, cold and have a high content of organic matter (10–25%). They differ in that they show no signs of a surface (Aₐ layer) accumulation of undecomposed or partly decomposed organic matter or of podsolization; they also have an appreciable content of clay (20–35%) and a relatively low C/N ratio (12–17). Because of the depth (up to 1 m) of these soils and their intimate mixture of mineral and humified organic matter, the Australian alps have been referred to as 'soil mountains' (Costin 1955, 1959) in contrast to the predominantly peaty or rocky surfaces of high mountains in Europe and New Zealand.

It has been suggested (Costin et al. 1952), that the vigorous growth of herbaceous vegetation, particularly of the snow grass (Poa caespitosa†), on these base-unsaturated alpine humus soils is made possible by rapid decomposition of organic matter leading to a rapid circulation of the limited bases and micro-nutrients. It has recently been shown that the rate of decomposition is more rapid in transitional alpine humus soils at 1520 m and alpine humus soils at 1890 m than in podsolic soils at 1290 m (Wood 1970, 1971).

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† Authorities for scientific names are given in Table 1.
The dominant group (in terms of biomass) of decomposer organisms in these soils are earthworms (Megascolecidae) and the present paper is concerned with their distribution and abundance in relation to soils and vegetation.

SITES

The sites were located on the eastern slopes of Mt Kosciusko in the Snowy Mountains and covered an altitudinal range from 910 m near Jindabyne to 2160 m near the summit of Mt Kosciusko (2225 m), a horizontal distance of approximately 37 km. Between the climatic extremes of Jindabyne, with an average annual precipitation of 560 mm and a mean annual temperature of 11°C, and the summit of Mt Kosciusko, with an average annual precipitation of 2285 mm and a mean annual temperature of 2°C, the vegetation and soils range from savanna woodland with grey-brown podsolic soils, dry sclerophyll forest with various kinds of podsolic soils, wet sclerophyll forests with transitional alpine humus soils to sub-alpine woodland and tall alpine herbfield with alpine humus soils. At Jindabyne precipitation is more or less evenly distributed throughout the year but with increasing altitude the proportion of winter precipitation (April–September) gradually increases. At high montane elevations (up to 1520 m) heavy falls of snow may occur during the winter months but usually snow does not lie continuously for more than 2–4 weeks. In the sub-alpine and alpine zones most of the winter precipitation occurs as snow which may lie for 3–8 months (leweward snow-patches sometimes persist throughout the summer), although the soils do not freeze and soil temperatures under the snow-cover remain between 0°C and 1°C (Wood 1970). Due to the relatively warm summer temperatures (mean monthly maxima in mid-summer are 15–24°C in sub-alpine regions and 10–15°C in alpine regions) and the high incidence of direct sunlight there is, in the alpine zone, a very rapid transition at the time of peak snow-melt from soil temperatures of near zero to temperatures of 12°C or higher (Wood 1971).

With the exception of sites 113 and 201, where the soils were developed on phyllite, the parent material at all sites is gneissic granite. Costin et al. (1952) and Costin (1954) made an extensive study of soils and weathering in a similar altitudinal sequence of soils developed on gneissic granite and discussed the changes observed in relation to climate and vegetation. Their nomenclature of soils is followed in this paper for two reasons. Firstly, there is no other published information on the soils of this region. Secondly, the alternative method of classification (Northcote 1965) which has been used extensively in Australia, does not lead to a meaningful grouping of these soils. In addition, as this paper demonstrated, the distribution of earthworms is closely related to the groups of soils as established by Costin et al. (1952) and Costin (1954). Nevertheless, the term ‘podsolic’ does not adequately describe two of the three groups of soils in the montane zone which have been given this name and the term ‘earth’ offers a better description with the three soil types being called grey-brown podsolic, reddish-brown (instead of ‘iron’) earth and brown earth.

Nomenclature of vegetation (Table 1) follows Costin (1954) except that the term ‘dry sclerophyll forest’ has been applied to the association of trees and shrubs at each particular site and not to the alliance. For instance, the association at sites 11, 206, 207 and 186 is dry sclerophyll forest although these associations occur within the Eucalyptus delegatensis—E. dalrympleana wet sclerophyll forest alliance (Costin 1954). A further difference is that the ‘snow gum’ (E. niphophylla Maiden and Blakely) which is characteristic of sub-alpine woodland (Costin 1954) is now recognized as one of the various forms of E. pauciflora.
Table 1. Distribution of Megascolecidae at sites on the eastern slopes of Mt Kosciusko (asterisk indicates occurrence of one individual only)

<table>
<thead>
<tr>
<th>Zone:</th>
<th>Montane</th>
<th>Sub-alpine</th>
<th>Alpine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation†:</td>
<td>S D D D D D D W W W SA SA SA SA H H H H H H H F</td>
<td>SA SA SA</td>
<td>H H H H H H H F</td>
</tr>
<tr>
<td>Soil:</td>
<td>Podsolic</td>
<td>Transitional alpine humus</td>
<td>Alpine humus soils</td>
</tr>
<tr>
<td>Grey-brown</td>
<td>Iron</td>
<td>Brown</td>
<td>B Horizon</td>
</tr>
<tr>
<td>Altitude: (m)</td>
<td>910 940 1140 1210 1290 1340 1340 1400 1520</td>
<td>1640 1790 1840 1890 1950 2100 2130 2140 2160 1980 2040 2100</td>
<td>1980 2040 2100</td>
</tr>
<tr>
<td>Site number</td>
<td>10 185</td>
<td>11 206 207</td>
<td>186 208 210 16 15 203 205 140 202 204</td>
</tr>
<tr>
<td>Topsoil species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptodrilus fastigatus Fletcher</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megascolex celmiiae Jamieson</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diporochaeta pheretima Jamieson</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subsoil species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oreoscolex imparicystis Jamieson</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Cryptodrilus tenuis Fletcher</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gralsophilus montiskosciuskoi Jamieson</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. woodi Jamieson</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vesiculodrilus frenchi (Spencer)</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. purpureus Jamieson</td>
<td>+ + + + + + + + + + + + + + + + + + + + + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of species excluding rare occurrences(*)</td>
<td>4 4 4 4 4 5 5 5 5 4 4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† S, Savanna woodland (Eucalyptus pauciflora Sieb. ex Spreng); D, dry sclerophyll forest (Eucalyptus pauciflora, E. rubida Deane and Maiden, E. stellulata Sieb. ex DC., E. dives Schau., E. dalrympleana Maiden); W, wet sclerophyll forest (Eucalyptus delegatensis R.T. Baker); SA, sub-alpine woodland (Eucalyptus pauciflora); H, tall alpine herbfield (Poa caespitosa Forst. f.s.lat., Celmisia longifolia Cass.); F, fjeldmarke (Epacris petrophila Hook f., Veronica densifolia F. Muell.).
Twenty-four sites in natural habitats were sampled for earthworms and quantitative samples were taken at eighteen of these. The distribution of sites in relation to soils and vegetation is shown in Table 1. Details of certain sites need further clarification. It will be noticed that the succession of soils iron podsolic—brown podsolic—transitional alpine humus does not follow an exact altitudinal sequence. This is because the 'low altitude' transitional alpine humus soils (sites 208, 210) are located closer to the main dividing range than the other sites under sclerophyll forest and, as the eastern slopes of Mt Kosciusko are in a 'rain-shadow', these two sites receive more rain than sites at similar altitudes (e.g. sites 11, 206, 207) which are further away from the main range. The effect of aspect is evident from sites 186 and 16 which are located at identical altitudes, on the opposite sides of a valley. The north-facing slope (site 186) exposed to the sun is drier (plant association is dry sclerophyll forest) than the shaded, south-facing slope (site 16, plant association is wet sclerophyll forest). Site 205 is located at Charlotte's Pass near a popular scenic lookout and ski-lift. The effect of excessive human trampling has led to death of the snow grass and the exposure of patches of bare soil surface and there are obvious effects on the earthworm population. The alpine humus soils developed on phyllite (sites 113, 201) are shallow (20–35 cm deep), very stony and located in zones of solifluction (Costin et al. 1967); one of these sites (113) is located on a steep (25–30°) north-facing slope and is much drier (see Table 2) than other alpine humus soils.

Several areas where native vegetation had been disturbed or destroyed were also sampled (non-quantitatively) for earthworms. These localities could be grouped into various categories as follows.

1. Felled *Eucalyptus* forest, herbaceous ground cover and leaf litter relatively undisturbed.
2. *Eucalyptus* forest felled, burnt, herbaceous ground cover and leaf litter destroyed and largely replaced by exotic plants.
3. Lawns and gardens.
4. Roadside clearings where *Eucalyptus* trees have been removed and the ground cover consists of a mixture of native and exotic species.

**METHODS**

**Soil analyses**

After removal of surface vegetation and litter, samples of soil from depths of 0–4 cm and 12–16 cm were taken for analysis. The following determinations were made on each sample: particle size analysis, pH (determined on a 1: 5 soil water suspension, Piper 1942), moisture content (determined gravimetrically on a wet-weight basis) and organic carbon (determined by Tinsley's (1950) method, slightly modified).

**Earthworm samples**

In natural habitats eighteen sites were sampled quantitatively for earthworms and a further six sites were sampled non-quantitatively. At each of the eighteen sites ten blocks of soil 25 x 25 cm (0.0625 m² surface area) were removed to a depth of 0.5–1.0 m (depending on the depth of the soil). The samples were spread on plastic sheets and earthworms removed by hand, transferred to 70% ethyl alcohol and weighed within 10 days of collection. All samples were taken between 25 February and 2 March 1969.

Although hand-sorting suffers from the disadvantage of being tedious and that small specimens may be missed (Nelson & Satchell 1962) and deep-burrowing species may escape
(Raw 1959) it has proved to be more efficient for some species of Lumbricidae than chemical-expulsion methods (Evans & Guild 1947; Nelson & Satchell 1962; Satchell 1969). Furthermore, it was the only possible method in the present studies which were conducted in areas remote from laboratories and the services required for employment of chemical-expulsion, wet sieving or flotation methods.

Raw (1962), Satchell (1969) and Pierce (1972) found that Lumbricidae lost between 10% and 25% of their weight after 7 days when preserved in 70% ethyl alcohol or 5% formalin and this factor must be considered when estimates of biomass are based on preserved specimens. A further source of error in estimating biomass of earthworms is that inclusion of the gut contents, particularly of species that ingest large amounts of soil, may lead to over-estimates of earthworm biomass. Satchell (1969) found that the gut contents of Lumbricus terrestris L. made up 20% of the fresh weight in small specimens and up to 41% in large specimens.

In the present studies loss in weight of megascolecid earthworms during preservation in 70% ethyl alcohol for 10 days varied from 9% of the fresh weight in small specimens to 43% in large specimens of Notoxocole montiskosciuskoi. Gut contents made up 5% of the fresh weight in small specimens to 55% in large specimens (7-9 g fresh weight) of N. montiskosciuskoi. The loss in weight during preservation was considered to be sufficiently close to the gain in weight by inclusion of gut contents that estimates of biomass were based on the weights of alcohol-preserved specimens including gut contents. It is possible that this method has lead to an over-estimate of the biomass of N. montiskosciuskoi by a factor of up to 12% due to the fact that the gut of this species contains considerable quantities of soil.

RESULTS

Soil analyses

The altitudinal trends in pH, moisture, organic carbon and coarse sand (Table 2) are similar to the trends established by Costin et al. (1952) and Costin (1954) in their more detailed investigation of a similar altitudinal sequence of soils. Soil pH ranges from over 7-0 at the lower elevations and gradually decreases with increasing altitude to 4-0 at the highest elevations and is obviously directly related to the parallel increase in precipitation and decrease in temperature. In contrast organic carbon contents are maximum in the sub-alpine and lower alpine zones between altitudes of 1520 m and 1650 m; soil moisture values rise sharply in the upper sub-alpine and alpine zone and are maximum in the lower alpine zone; coarse sand contents are lowest in the sub-alpine and alpine zones between altitudes of 1520 m and 2040 m.

Distribution of species

There have been several ecological classifications of earthworms according to their preferences for certain soil conditions or soil horizons. British Lumbricidae were classified into three groups by Satchell (1955) according to their occurrence in soils of different pH. Of the thirteen species he investigated three, all surface-inhibiting species, were ‘acid-tolerant’ (pH < 4-5); five, all subsoil-inhabiting species, were ‘acid-intolerant’ (absent in soils with pH < 4-5); five others, consisting of two surface dwellers, two subsoil dwellers and one which lives in both situations, were ‘ubiquitous’ being found in soils with pH values of <4-0-7-0. Surface-inhabiting species are generally well-pigmented in contrast to the paler subsoil dwellers. Lee (1959) classified the New Zealand Megascol-
Table 2. Vegetation and soil characteristics of sites on Mt Kosciusko sampled for Megascolecidae

<table>
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<tbody>
<tr>
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<td>1140</td>
<td>1290</td>
<td>1340</td>
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<td>11</td>
<td>206</td>
<td>207</td>
<td>186</td>
<td>208</td>
<td>210</td>
<td>16</td>
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<tr>
<td>Soil pH 0-4 cm</td>
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<td>7·2</td>
<td>5·7</td>
<td>6·0</td>
<td>5·8</td>
<td>5·2</td>
<td>5·3</td>
<td>4·8</td>
<td>5·7</td>
</tr>
<tr>
<td>Soil pH 12-16 cm</td>
<td>6·6</td>
<td>6·9</td>
<td>5·5</td>
<td>5·9</td>
<td>5·6</td>
<td>5·1</td>
<td>5·4</td>
<td>4·8</td>
<td>5·9</td>
</tr>
<tr>
<td>Organic carbon (%) 0-4 cm</td>
<td>1·5</td>
<td>1·4</td>
<td>1·7</td>
<td>3·3</td>
<td>4·4</td>
<td>4·1</td>
<td>5·6</td>
<td>4·7</td>
<td>6·5</td>
</tr>
<tr>
<td>Organic carbon (%) 12-16 cm</td>
<td>0·3</td>
<td>0·4</td>
<td>0·8</td>
<td>0·9</td>
<td>1·3</td>
<td>1·0</td>
<td>2·3</td>
<td>2·4</td>
<td>3·1</td>
</tr>
<tr>
<td>Soil moisture (%) 0-4 cm</td>
<td>11</td>
<td>9</td>
<td>14</td>
<td>17</td>
<td>15</td>
<td>21</td>
<td>17</td>
<td>18</td>
<td>31</td>
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<tr>
<td>Soil moisture (%) 12-16 cm</td>
<td>12</td>
<td>7</td>
<td>11</td>
<td>13</td>
<td>17</td>
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<td>50</td>
<td>48</td>
<td>38</td>
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<tr>
<td>Coarse sand (%) 12-16 cm</td>
<td>67</td>
<td>69</td>
<td>56</td>
<td>63</td>
<td>59</td>
<td>55</td>
<td>63</td>
<td>44</td>
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ecidae (178 species) into three groups—a ‘leaf mould’ group, a ‘topsoil’ group and a ‘subsoil’ group. The leaf mould group comprised species which are small (15–180 mm long), active, heavily pigmented and often very thick in proportion to their length, due to the great thickness of muscle layers in the body wall. Species in this group do not construct burrows but move freely in available spaces in their environmental media. The topsoil group comprised species which are larger (25–300 mm), well-pigmented but less so than leaf-mould species and also less active and relatively longer than leaf-mould species. Species in this group make burrows and leave them only to forage in the leaf mould as opposed to leaf mould species which live permanently in the surface leaf litter. Subsoil earthworms were described as being larger (32–1400 mm), slow-moving, unpigmented or only lightly pigmented, with muscles of the body wall being weakly developed. Species in this group ingest relatively large amounts of soil and only occasionally come to the surface for food. Similar classifications of European Lumbricidae into epigeal, topsoil and subsoil species were made by Bouche (1971, 1972) and Wilcke (1953).

Knowledge of Australian Megascolecidae is so scant that a similar classification has never been made and cannot be made until the fauna has been studied in more detail. As far as the Kosciusko fauna is concerned soil pH does not appear to have the dominant rôle in determining the distribution of species as it does with European Lumbricidae. However, it is possible to recognize three groups of species: ‘topsoil’ species which are active, heavily pigmented, live in the topsoil and leaf litter and do not make burrows in the subsoil; ‘subsoil’ species which are less active, pale, live in the subsoil and topsoil but are rarely, if ever, found in the surface litter; ‘other’ species which have the physical characteristics of the topsoil species (i.e. active, heavily pigmented) but which live in semi-permanent vertical burrows extending from the surface, where they feed, to the subsoil. This latter group would be included in the ‘topsoil’ group of the classifications mentioned above, but their distinctive burrowing behaviour is sufficiently characteristic to justify including them in a separate group. Among Lumbricidae, species such as Lumbricus terrestris have similar burrowing habits.

The distribution of the ten species (described or re-described by Jamieson 1972) of Megascolecidae found in the present study is shown in Table 1, their density and biomass in Fig. 1 and Fig. 2 and their relative abundance above and below a depth of 15 cm is shown in Table 3. There is so little known about the biology and habits of Australian Megascolecidae that brief notes on each species are made below. Their vertical distribution in any particular soil and their burrowing and feeding behaviour are paralleled in their better known European counterparts, the Lumbricidae. Two aspects of the behaviour of the Kosciusko Megascolecidae which contrast with certain Lumbricidae, are worth noting. Firstly, none of the surface-feeding species drag leaf litter into their burrows, and secondly, none of the species cast on the surface but do so within the soil.

**Topsoil species**

*Cryptodrilus fastigatus* is a reddish-purple, darkly pigmented species up to 130 mm in length. It occurs throughout the range of soils included in this study and is often the most abundant species. It is exclusively a topsoil species (only a single specimen has been found below 15 cm—see Table 3) and is often found burrowing just below the surface leaf litter.

*Megascolex celmisiae* is a reddish, moderately pigmented species up to 90 mm in length. It occurs throughout the range of soils included in this study and at some sites is more abundant than *Cryptodrilus fastigatus*. It is principally a topsoil species being
most numerous below the surface leaf litter but occasionally penetrates into the subsoil (Table 3).

_Diphorochaeta pheretima_ is a small (40 mm), darkly pigmented species which has only been found at one of the sites. It could possibly be included in the 'leaf mould' (Lee 1959) or 'epigeal' (Bouché 1971, 1972) group.

**Subsoil species**

_Notoscolex montiskosciuskoi_ is the 'mountain earthworm (Megascole sp.)' mentioned by Costin _et al._ (1952) and Costin (1954). It is a long (up to 200 mm), thick (up to 20 mm), slow-moving pale grey species which moves throughout the full depth of the soil profile. It has a spiral gut which is obviously an adaptation to its nutrient-poor food which consists predominantly of soil. It occurs throughout the range of soils included in this study.

_Oreoscolex imparicystis_ is a relatively long (up to 140 mm), slender (up to 8 mm thick), fairly active, pale grey species which occurs in subsoil and lower topsoil. It may
occasionally feed under the surface leaf litter but its gut contents consist largely of soil. It has a very restricted distribution being found only in transitional alpine humus soils under *Eucalyptus delegatensis* wet sclerophyll forest and in similar soils (brown podsolics) under *E. dalrympleana–E. pauciflora* forest (site 207).

*Cryptodrilus tenuis* is a small (up to 55 mm in length), slender (4–5 mm thick), inactive, pale grey species which occurs in subsoil and lower topsoil. It does not feed under the surface leaf litter and its gut contents consist largely of soil. It has a restricted distribution being found only in podsollic soils with low organic carbon content under dry sclerophyll *Eucalyptus* forest.

*Graliophilus woodi* is a moderately long (up to 110 mm), slender (up to 6–7 mm thick), fairly active, pale grey species which can be regarded as the counterpart of *Oreoscolex imparicystis* in alpine humus soils. It moves throughout the full depth of the profile and

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**Fig. 2.** Biomass of different species of Megascolecidae in soils on the eastern slopes of Mt Kosciusko. (a) *Cryptodrilus fastigatus*; (b) *Megascolex celmisiae*; (c) *Notoscolex montiskosciukoi*; (d) *Oreoscolex imparicystis*; (e) *Cryptodrilus tenuis*; (f) *Graliophilus woodi*; (g) *Vesiculodrilus frenchi*; (h) *V. purpureus*. 
Table 3. Depth distribution of Megascolecidae in montane and alpine soils on the eastern slopes of Mt Kosciusko (figures are percentage of population above 15 cm)

<table>
<thead>
<tr>
<th>Soil:</th>
<th>Podsolic</th>
<th>Transitional</th>
<th>Alpine humus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grey-brown</td>
<td>Iron</td>
<td>Brown</td>
</tr>
<tr>
<td>Site number:</td>
<td>10 185</td>
<td>11 206</td>
<td>207 186</td>
</tr>
<tr>
<td>Topsoil species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptodrilus fastigatus</td>
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<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Megascolex celmaniae</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Subsoil species</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Notoscolex montiskosciuskoi</td>
<td>100 100</td>
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<td>66</td>
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<tr>
<td>Oreoscolex imparicystis</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Cryptodrilus tenuis</td>
<td>50 50</td>
<td>40</td>
<td>60</td>
</tr>
<tr>
<td>Gallophilus woodi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vesiculodrilus frenchi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. purpureus</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
T. G. Wood

is sometimes found feeding under the surface root mat of *Poa* tussocks and among the sub-surface rhizomes of *Celmisia longifolia*.

*Graliophilus montiskosciuskoi* is known from only one specimen. It is possibly a sub-soil species.

**Other species (surface-feeding/deep-burrowing)**

*Vesiculodrilus purpureus* is a reddish-purple darkly pigmented species up to 150 mm in length and 10 mm thick. It lives in semi-permanent, vertical burrows which penetrate deep into the subsoil to the weathering surface of the parent material. Apart from a single specimen found in a podsolic soil at an altitude of 1290 m (site 11), it is confined to a narrow altitudinal range encompassing transitional alpine humus soils at 1520 m and alpine humus soils in the sub-alpine zone (i.e. in alpine humus soil with a B horizon). As it can withdraw rapidly down its burrow when disturbed it is likely to be overlooked by extraction methods employing digging and hand-sorting. On the other hand, it is rapidly expelled by chemical extraction methods utilizing formalin or potassium permanganate. Its feeding habits have not been observed, but its dark pigmentation suggests that, like *Vesiculodrilus frenchi* (see below), it emerges from its burrow in the evening or at night to feed on surface leaf litter. There is no evidence that it drags leaf litter or other organic debris down its burrow as does the well-known lumbricid *Lumbricus terrestris*.

*Vesiculodrilus frenchi* is a reddish-purple, darkly pigmented species up to 100 mm in length and 7–8 mm thick. It is a smaller species than *V. purpureus* but with similar habits in that it lives in semi-permanent vertical burrows extending from the surface to the weathering parent material. It has been found only in alpine humus soils in the treeless alpine zone above 1890 m (i.e. in alpine humus soils lacking a B horizon) and its distribution does not overlap that of *V. purpureus*. It appears to be rare in alpine humus soils developed on phyllite. It is, like *V. purpureus*, rapidly expelled by chemical extraction methods but due to the shallower depth (<60 cm) of alpine humus soils in the alpine zone it is more readily found by digging/hand-sorting than is *V. purpureus* which is found in the deeper alpine humus soils (>90 cm) in the sub-alpine zone. It emerges from its burrow at night, particularly after rain, to feed either on the surface of the alpine herbfield or in the surface litter or sub-surface rhizomes of *Celmisia longifolia*. It does not drag leaf litter down its burrows.

Of the ten species recorded from these sites two are extremely rare being known from only one site each and three occur throughout the full range of sites studied. The five remaining species have distinct distributions closely related to soils and vegetation. Of the three subsoil species, *Cryptodrilus tenuis* is characteristic of podsolic soils under dry sclerophyll forest, *Oreoscolex imparicystis* is characteristic of transitional alpine humus soils and brown podsoles under wet sclerophyll forest and *Graliophilus woodi* is characteristic of alpine humus soils. Of the two surface-feeding/deep-burrowing species *Vesiculodrilus purpureus* is found below the alpine zone in alpine humus soils with a B horizon, transitional alpine humus soils and rarely in podsolic soils, while *V. frenchi* is found only in alpine humus soils (lacking a B horizon) in the alpine zone. Thus, ignoring the two rare species and the rare occurrence of *Cryptodrilus tenuis* in brown podsolic and *Vesiculodrilus purpureus* in iron podsolic soils, there are similar numbers of species (four or five) in each soil type (Table 1). The soils can, therefore, be characterized by the distinct distribution of the three subterranean species and the two surface-feeding/deep-burrowing species.
Table 4. Density (numbers/m²) and biomass (g/m²) of Megascolecidae in sites on the eastern slopes of Mt Kosciusko

<table>
<thead>
<tr>
<th>Soil type:</th>
<th>Podsolics</th>
<th>Transitional Alpine humus</th>
<th>Alpine humus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grey-brown</td>
<td>Iron</td>
<td>Brown</td>
</tr>
<tr>
<td>Site number:</td>
<td>10 185</td>
<td>11 206</td>
<td>207 186</td>
</tr>
<tr>
<td>Density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topsoil species</td>
<td>32</td>
<td>16</td>
<td>256</td>
</tr>
<tr>
<td>Subsoil species</td>
<td>9-6</td>
<td>5-6</td>
<td>6-4</td>
</tr>
<tr>
<td>Total</td>
<td>13-8</td>
<td>7-2</td>
<td>32-0</td>
</tr>
<tr>
<td>Biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topsoil species</td>
<td>0-6</td>
<td>0-5</td>
<td>3-7</td>
</tr>
<tr>
<td>Subsoil species</td>
<td>0-6</td>
<td>0-8</td>
<td>8-2</td>
</tr>
<tr>
<td>Total</td>
<td>10-2</td>
<td>1-3</td>
<td>11-9</td>
</tr>
</tbody>
</table>

* These values include figures for Vesiculodrilus purpureus.
† These values include figures for V. frenchi.
Abundance and biomass

The population density and biomass of topsoil and subsoil groups is shown in Table 4 and for individual species in Figs. 1 and 2. In general, earthworms are more abundant and have a greater biomass in the alpine humus and transitional alpine humus soils than in the podsolic soils. This greater abundance is due mainly to topsoil species, as the abundance of subsoil species is not markedly different in the three major groups of soils. The greater biomass of topsoil species in alpine humus of the alpine zone is due partly to their greater abundance and partly to the fact that the average size of Cryptodrilus fastigatus is greater in these soils (Table 5). The greater biomass of subsoil species in transitional alpine humus and alpine humus soils is due partly to the fact that C. tenuis is much smaller than Oreoscolex imparicystis and Graliophilus woodi and partly to the greater average size of Notoscolex montiskosciuskoi in alpine humus soils (Table 5).

Three of the alpine humus soils (sites 205, 113 and 201) have low earthworm populations. Site 205 has been subjected to excessive human trampling resulting in death of the snow grass and exposure of bare soil surface. The numbers and biomass of the topsoil species are very low but it is only one of the two species, Cryptodrilus fastigatus (3-2/m² and 0-37 g/m²), which is affected, whereas Megascolex celmisiae is relatively abundant (12-0/m²) and its biomass (5-4 g/m²) is exceeded in only two other sites (204, 201). It is not surprising to find that topsoil species are affected by partial destruction of ground cover and the surface litter, but the complete absence of subsoil earthworms, which one might expect to be relatively unaffected by such disturbances, is not readily explained. Possibly, excessive trampling has led to compaction and a change in the structure and moisture regime of the subsoil. The low earthworm population at this site would appear to confirm other evidence (Costin 1954, 1959) suggesting that these high altitude communities are very susceptible to apparently minor stresses. Sites 113 and 201 are both developed on phyllite and it has already been noted that these soils are relatively shallow, stony and subject to solifluction. Site 113, which had an extremely low population (8-0/M²) and biomass (1-17 g/m²) of earthworms at the time of sampling, is located on a steep slope (25-30°) and is very dry in summer (sub-surface soil moisture is similar to that in soils of the upper montane zone—see Table 2) and in fact Megascolex celmisiae was the only species present, although Graliophilus woodi and Notoscolex montiskosciuskoi have been found at this site on other occasions (T. G. Wood, unpublished). Megascolex celmisiae was also the most abundant species at site 201 and its biomass was only slightly exceeded by the large, subsoil species Notoscolex montiskosciuskoi. The relative abundance of Cryptodrilus fastigatus and Megascolex celmisiae in these three alpine humus soils suggest that M. celmisiae becomes dominant when Cryptodrilus fastigatus is scarce and in fact there was a significant negative correlation ($r = -0.84**$) between the biomasses of these two species in the eight alpine humus soils where the two species co-exist.

Table 5. Mean weight (g) of three species of Megascolecidae in relation to altitudinal sequence of soils on the eastern slopes of Mt Kosciusko

<table>
<thead>
<tr>
<th>Zone: Soil:</th>
<th>Montane Podsolics</th>
<th>Transitional Alpine humus</th>
<th>Sub-alpine Alpine humus</th>
<th>Alpine Alpine humus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptodrilus fastigatus</td>
<td>0·214 ± 0·051</td>
<td>0·188 ± 0·032</td>
<td>0·197 ± 0·053</td>
<td>0·349 ± 0·060</td>
</tr>
<tr>
<td>Megascolex celmisiae</td>
<td>0·126 ± 0·040</td>
<td>0·116 ± 0·025</td>
<td>0·225 ± 0·095</td>
<td>0·149 ± 0·021</td>
</tr>
<tr>
<td>Notoscolex montiskosciuskoi</td>
<td>1·601 ± 0·851</td>
<td>1·324 ± 0·555</td>
<td>2·024 ± 0·424</td>
<td>3·346 ± 0·398</td>
</tr>
</tbody>
</table>
The abundance and biomass of earthworms appear to follow the trend in certain soil properties in being maximal in the upper sub-alpine and lower alpine zone. Correlation coefficients between the biomass of topsoil earthworms, subsoil earthworms and the three widely ranging species and the values for moisture, coarse sand and organic carbon are shown in Table 6. Three sites have been omitted from these calculations: the two sites on phyllite (113, 201) and site 205 (see above). The biomasses of topsoil species are highly positively correlated with soil moisture but this is due entirely to *C. fastigatus*. The biomasses of both of the topsoil species, *C. fastigatus* and *M. celmisiae*, are negatively correlated with coarse sand and positively correlated with organic carbon. Biomass of subsoil species and *Notoscolex montiskosciuskoi* are correlated only with organic carbon.

Table 6. Correlation coefficients (r) between biomass of topsoil- and subsoil-inhibiting *Megascolecidae* and topsoil (0-4 cm) and subsoil (12-16 cm) contents of moisture, coarse sand and organic carbon (data in Tables 1, 4 and Fig. 2)

<table>
<thead>
<tr>
<th>Topsoil species—total</th>
<th>Moisture</th>
<th>Coarse sand</th>
<th>Organic carbon</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cryptodrilus fastigatus</em></td>
<td>0.954***</td>
<td>-0.648*</td>
<td>0.630*</td>
</tr>
<tr>
<td><em>Megascolex celmisiae</em></td>
<td>0.916***</td>
<td>-0.655*</td>
<td>0.599*</td>
</tr>
<tr>
<td>Subsoil species—total</td>
<td>0.337</td>
<td>-0.248</td>
<td>0.101</td>
</tr>
<tr>
<td><em>Notoscolex montiskosciuskoi</em></td>
<td>0.472</td>
<td>-0.547</td>
<td>0.653*</td>
</tr>
</tbody>
</table>

* r significant at 5% level, *** at 0.1% level.

Table 7. Effect of vegetation cover on abundance (numbers/m²) of *Megascolecidae* in montane, sub-alpine and alpine soils on the eastern slopes of Mt Kosciusko

<table>
<thead>
<tr>
<th>Vegetation†:</th>
<th>Dry and wet sclerophyll forest</th>
<th>Sub-alpine woodland</th>
<th>Tall alpine herbfield</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cover-type:</td>
<td><em>Poa</em> grass</td>
<td><em>Eucalyptus</em> litter</td>
<td><em>Poa caespitosa</em></td>
</tr>
<tr>
<td><em>Cryptodrilus fastigatus</em></td>
<td>6.4</td>
<td>8.4</td>
<td>71.2***</td>
</tr>
<tr>
<td><em>Megascolex celmisiae</em></td>
<td>6.4</td>
<td>3.6</td>
<td>20.8***</td>
</tr>
<tr>
<td>Total—topsoil species</td>
<td>12.8</td>
<td>12.0</td>
<td>92.0***</td>
</tr>
<tr>
<td><em>Notoscolex montiskosciuskoi</em></td>
<td>4.8</td>
<td>10.0</td>
<td>4.0</td>
</tr>
<tr>
<td><em>Oreoscolex imparicystis</em></td>
<td>8.4</td>
<td>12.4</td>
<td></td>
</tr>
<tr>
<td><em>Cryptodrilus tenius</em></td>
<td>4.8</td>
<td>8.8</td>
<td>3.2</td>
</tr>
<tr>
<td><em>Gralipohilus woodi</em></td>
<td>18.0</td>
<td>31.2*</td>
<td>7.2</td>
</tr>
</tbody>
</table>

* Difference between cover-types within vegetation significant at 5% level, *** at 0.1% level.
† Dry and wet sclerophyll forest: sites 206, 207, 208, 210; sub-alpine woodland: sites 203, 205; tall alpine herbfield: sites 201, 202, 204 (five samples (0.0625 m² area) from each cover-type at each site).

The nature of the ground-cover in natural situations did not appear to have a significant effect on the numbers of earthworms (Table 7). In sclerophyll forest, the only effect was on subsoil earthworms which were significantly more abundant under a cover of *Eucalyptus* litter than under a cover of *Poa*, although there were no significant individual effects on the three subsoil species. In alpine herbfield there were no significant differences between the numbers of earthworms under *Poa* or under *Celmisia*. In sub-alpine woodland both of the topsoil species, *Cryptodrilus fastigatus* and *Megascolex celmisiae*, were more abundant under trees than in the open between trees but there was no effect on subsoil species.
Table 8. Changes in the earthworm fauna associated with changes in vegetation in the Koskiusko National Park

<table>
<thead>
<tr>
<th>Habitat:</th>
<th>Felled Eucalyptus forest – native ground cover</th>
<th>Eucalyptus forest felled, burnt – exotic ground cover</th>
<th>Lawns and gardens</th>
<th>Roadside clearing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m):</td>
<td>890</td>
<td>890</td>
<td>890</td>
<td>1220</td>
</tr>
<tr>
<td>Topsoil species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megascolecidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptodrilus fastigatus</td>
<td>+</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Megascolex celmisae</td>
<td>+</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Lumbricidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lumbricus rubellus (Hoff.)</td>
<td>.</td>
<td>.</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Eisenea rosea (Sav.)</td>
<td>.</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Subsoil species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megascolecidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Notoscolex montiskosciuskoi</td>
<td>+</td>
<td>+</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Cryptodrilus fastigatus</td>
<td>+</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Lumbricidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Octolasium cyaneum (Sav.)</td>
<td>.</td>
<td>+</td>
<td>+</td>
<td>.</td>
</tr>
<tr>
<td>Allolobophora terrestris f. longa (Ude)</td>
<td>.</td>
<td>+</td>
<td>+</td>
<td>.</td>
</tr>
</tbody>
</table>
In contrast, the change from native to exotic vegetation was accompanied by marked changes in the earthworm fauna. These changes were not quantified but the data in Table 8 show there is a more or less complete change from a native fauna of Megascolecidae to an exotic fauna of Lumbricidae, once the native ground cover and litter have been destroyed. The two topsoil species, Cryptodrilus fastigatus and Megascolex celmsiae, were replaced by Lumbricus rubellus and Eisenia rosea. Of the subsoil species, Cryptodrilus tenuis disappeared completely, although Notoscolex montiskosciukoi was able to survive alongside the exotic Octolasion cyaneum and Allolobophora terrestris f. longa.

DISCUSSION

Distribution of species

Alpine humus soils on Mt Kosciusko appear to provide an unusually favourable habitat for earthworms, in that they support a similar number of species (four or five) to soils at lower elevations. This contrasts with species/altitude relationships in other parts of the world where the number of species decreases with altitude. Lee (1959) found that there was an inverse relationship between number of species of Megascolecidae and altitude on mountains in the North Island of New Zealand until in the tussock grassland mountain tops of the Rimutaka-Tararua range there was only one species present. Boucé (1972) recorded fifteen species of Lumbricidae above 1500 m in France, seven above 200 m and four above 2500 m. In the Chernogora region of Russia, Sergienko (1969) found five species of Lumbricidae at an altitude of 740 m, four species at 1000 m, three species at 1300 m and one species at 1600–1800 m.

There is little information on the distribution within Australia of the species recorded in the present investigations. Cryptodrilus fastigatus was recorded from Illawara and Burrawang in New South Wales (Fletcher 1889) and Vesiculodrilus frenchi was recorded from Croajingolong in the mountainous area of East Gippsland (Spencer 1892). Fletcher (1889) recorded Cryptodrilus tenuis from Braidwood (New South Wales) and it is therefore likely that its range extends from the lower montane zone across the Monaro Tableland.

Abundance and biomass

There are no other published figures for the abundance of Megascolecidae in natural habitats in Australia. In irrigated pastures near Deniliquin (N.S.W.) population densities of a single species, Microscolex dubius (Fletcher), reached 32/m² (Barley & Kleinig 1964) and 14/m² (Noble, Gordon & Kleinig 1970). In New Zealand, Smith (1887) and Lee (1958) recorded population densities of 99/m² and 25–74/m² respectively in tussock grassland and Stockdill (1966) recorded a density of apparently a single-species population in sown (i.e. exotic) pasture of 205/m². In the Kosciusko sites population densities ranged from 7 to 135/m² and biomasses from 1 to 82g/m² although larger densities have been obtained on other occasions, the maximum being 184/m² (71 g/m²) at site 16 in December 1966 (T. G. Wood, unpublished). These maximum populations and biomasses are lower than have been recorded for Lumbricidae (524/m² and 152 g/m²) in natural and semi-natural forests and grasslands in Britain (Satchell 1967). Even greater populations of Lumbricidae have been recorded from exotic pastures in New Zealand (650–1400/m² and 140–320 g/m², Waters 1955) and southern Australia also supports substantial populations (260–740/m² and 39–152 g/m², Barley 1959; 247/m², Barley & Kleinig 1964;
357/m² and 80 g/m², Noble et al. 1970). It is surprising that more is known about the abundance of introduced Lumbricidae in New Zealand (for references see Stockdill 1966) and Australia (loc. cit.) than of the native Megascolecidae.

The altitudinal trend in abundance and biomass on Mt Koskiusko, with maxima in the lower alpine and upper sub-alpine zones and minima at low altitudes, contrasts with trends in other mountainous areas. According to Lee (1959) the abundance of Megascolecidae on mountains in the North Island of New Zealand decreases with increasing altitude and Sergienko (1969) found a decrease in biomass of Lumbricidae in the Chernogora region of Russia from 16.5 g/m² at 1000 m to 2.2 g/m² at 1800 m. It is likely that the predominantly skeletal and peaty soils of mountains in New Zealand and Europe provide a less favourable habitat for earthworms than the deep organo-mineral alpine humus soils on Mt Kosciusko, although as far as Lumbricidae are concerned there is the adverse effect of low pH (which tends to decrease with increasing altitude) to be considered.

The altitudinal trends in earthworm numbers and biomass, particularly the topsoil species, is closely related to trends in soil moisture, organic carbon and particle size distribution (Tables 2 and 6). The particle size distribution in a similar altitudinal sequence of soils developed on gneissic granite has been explained (Costin et al. 1952; Costin 1954) in terms of a balance between the production of large particles (i.e. coarse sand) by physical weathering and their breakdown to finer particles (i.e. silt, clay) by chemical weathering. Coarse sand contents are maximum in the lower montane zone where chemical weathering is limited by low soil moisture and decrease with increasing soil moisture to minimum values in the upper sub-alpine and lower alpine zone. In the upper alpine zone coarse sand contents rise as chemical weathering becomes limited by low temperatures although soil moisture is adequate. The altitudinal trend in soil organic carbon contents were also interpreted in terms of the combined effects of moisture and temperature on plant growth and decomposition processes, resulting in maximum plant growth, decomposition and soil organic carbon in the upper sub-alpine and lower alpine zones. Apparently these factors also favour earthworm populations and also the size of two of the three species which cover the full altitudinal range of sites. The smaller size of Notoscolex montiskoskiusko in the montane zone (Table 5) was obvious in the field and as this species ingests large quantities of soil, the size of this species may be directly related to soil organic carbon content.

Effects of vegetation

There are two aspects to the effects of vegetation on the distribution and abundance of earthworms: the effects of density of cover and the effects of type of cover.

Partial destruction of snow grass by excessive trampling was suggested as being directly (or indirectly through effects, such as compaction, on soil properties) responsible for the extremely low density (15.2/m²) and biomass (5.7 g/m²) of earthworms at site 205. There is no experimental evidence to support this suggestion although Chappell et al. (1971) found that excessive trampling on chalk grassland in Britain lead to a reduction in numbers of most groups of soil animals and the numbers and biomass of Lumbricidae were reduced from 103/m² (23.3 g/m²) to 22/m² (14.1 g/m²). These authors noted that trampling appeared to have more drastic effects on soil fauna than cutting or grazing, a conclusion of obvious significance for the management of popular National Parks such as Kosciusko.

There is little information on the effect of type of plant cover on earthworm popula-
tions in natural habitats. At Kosciusko the mosaic of grass cover/Eucalyptus litter cover in sclerophyll forest and Poa cover/Celmisia cover in alpine herbfield appeared to have little or no effect on earthworm populations but in sub-alpine woodland there were much greater numbers of earthworms under trees than in the open between trees. The greater abundance of topsoil species under trees is probably related to the fact that the trees intercept moisture in the form of snow, rain or cloud which results in greater precipitation under trees; this increase in moisture and the addition of nutrients (by foliar leaching) leads to a more vigorous growth of snow grass under trees (Costin et al. 1961; Costin & Wimbush 1961).

Drastic changes in the earthworm population follow the clearing of native vegetation and the invasion of cleared areas by exotic plants. Although few such areas were studied in the Kosciusko Park the complete changes in the topsoil fauna from two species of Megascolecidae to two species of Lumbricidae was very distinct and probably takes place fairly rapidly after the change in vegetation. Subsoil species of Lumbricidae also appear rapidly to invade these areas although the native subsoil species, Notoscolex montiskosciuskoi, appears to survive in some of these areas. The Lumbricidae have not been found in undisturbed native vegetation which suggests that the total or near-total disappearance of Megascolecidae in disturbed areas is due to the change from native to exotic vegetation and destruction of surface litter and not to competition from Lumbricidae. Lee (1959) made more detailed studies of similar changes in earthworm populations in New Zealand following the clearing and burning of native vegetation and suggested that competition between Lumbricidae and Megascolecidae was unlikely under most situations. The possible exception was Pinus plantations, where native species appeared to survive and co-exist with species of Lumbricidae which had invaded such areas.

ACKNOWLEDGMENTS

It is a pleasure to thank Dane and Robyn Wimbush for their hospitality, Mr N. C. Gare (Superintendent) of the Kosciusko National Park for permission to carry out these investigations within the Park and Mr R. George for assistance in the field. Grateful thanks are also extended to Dr B. G. M. Jamieson for identifying the earthworms.

SUMMARY

(1) An altitudinal sequence (910–2160 m) of soils developed on gneissic granite on the slopes of Mt Kosciusko passes successively through podsolic soils under dry sclerophyll Eucalyptus forest, transitional alpine humus soils under wet sclerophyll Eucalyptus forest to alpine humus soils under sub-alpine woodland and tall alpine herbfield (Poa–Celmisia).

(2) Ten species of earthworms were found in the soils. Two species were rare and the distribution of the other eight species resulted in each soil type having four to five species. The two topsoil species, Cryptodrilus fastigatus and Megascolex celsimiae and one of the subsoil species, Notoscolex montiskosciuskoi, were found over the full altitudinal range. Three other subsoil species characterized the soils: Cryptodrilus tenuis in podsolic soils with a low content of organic matter, Oreoscolex imparicystis in brown podsolic and transitional alpine humus soils and Graliophilus woodi in alpine humus soils. The two other species are surface-feeding and deep-burrowing: Vesiculodrilus purpureus is characteristic of transitional alpine humus soils and alpine humus soils.
with a B horizon and *Vesiculodrilus frenchi* is characteristic of alpine humus soils without a B horizon.

(3) Numbers and biomass increased from 7.2–32.8/m² (1.3–25.5 g/m²) in podsolic soils to 34.4–76.0/m² (12.3–47.9 g/m²) in transitional alpine humus soils and 39.2–134.8/m² (26.3–81.8 g/m²) in alpine humus soils. Maximum numbers and biomass were reached in the upper sub-alpine and lower alpine zones and were positively correlated with soil moisture and soil organic carbon and negatively correlated with coarse sand content. Individuals of *Cryptodrilus fastigatus* and *Notoscolex montiskoscuskoi* in alpine humus soils were larger than individuals of the same species in podsolic soils. At one alpine humus site excessive human trampling appeared to be responsible for the low population density (15.2/m²) and biomass (5.7 g/m²). The two alpine humus soils developed on phyllite also had low numbers (8.0–41.6/m²) and biomass (1.2–17.6 g/m²).

In alpine humus soils there was a strong negative correlation between the biomasses of the two topsoil species, *Cryptodrilus fastigatus* and *Megascolex celmisiae*. In alpine humus soils under sub-alpine woodland numbers were greater under trees (92.0/m²) than in the open between trees (8.0/m²).

(4) In dry sclerophyll forest the effect of felling trees, destruction of the natural ground cover and surface leaf litter and colonization by exotic herbaceous vegetation resulted in disappearance of the two topsoil species, *Cryptodrilus fastigatus* and *Megascolex celmisiae*, and their replacement by the lumbricids *Lumbricus rubellus* and *Eisenia rosea*. The native subsoil species *Cryptodrilus tenuis* also disappeared but *Notoscolex montiskoscuskoi* was able to survive alongside the lumbricids *Octolasium cyaneum* and *Allobophora terrestris f. longa*.

REFERENCES


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